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CIRCUMSCRIPTION OF *ECHINOCEREUS ARIZONICUS* SUBSP. *ARIZONICUS*: PHENETIC ANALYSIS OF MORPHOLOGICAL CHARACTERS IN SECTION *TRIGLOCHIDIATUS* (CACTACEAE), PART II

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Abstract

A multivariate analysis was performed for populations of *Echinocereus* (section *Triglochidiatus*) to facilitate the taxonomic circumscription of *E. arizonicus* subsp. *arizonicus*. Twenty-one morphological characters for 16 populations evidenced the validity of at least two subspecific taxa within *E. arizonicus*: *E. arizonicus* subsp. *arizonicus* and *E. arizonicus* subsp. *nigrihorridispinus*. Principle components analysis indicated that stem characters were most diagnostic in defining two distinct groups of populations, each including the type locality of one of the two subspecies. Unweighted pair group method with arithmetic mean (UPGMA) clustered populations of the two subspecies apart from one another and from those of the outgroup, *E. triglochidiatus* subsp. *mojavensis*. For most measured characters, means differed significantly between the two subspecies. Discriminant analysis correctly classified 97.0% for individuals of *E. arizonicus* subsp. *arizonicus* and 94.7% for individuals of *E. arizonicus* subsp. *nigrihorridispinus*, compared to an overall 97.8% correct classification of individuals for all perfect-flowered taxa of section *Triglochidiatus* investigated.

Key Words: *Echinocereus arizonicus*, section *Triglochidiatus*, multivariate analysis, morphological characters.

Taxonomy within section *Triglochidiatus* H. Bravo of *Echinocereus* Engelm. in F. A. Wislizenus has vacillated dramatically over the past few decades. The present study evaluates the circumscription of *E. arizonicus* Rose ex Orcutt subsp. *arizonicus* using multivariate techniques to compare morphological variation within populations to that among populations. It is the second portion of an ongoing phenetic analysis of section *Triglochidiatus*, the first of which addressed the recently discovered species, *E. yavapaiensis* M. A. Baker, and summarized the current knowledge of polyploidy within the section (Baker 2006). The taxonomic status of *E. arizonicus* subsp. *arizonicus*, which is federally listed as Endangered, has importance for conservation efforts because of threats from mining and other human related impacts.

Until recently, the most widely recognized treatment of *Echinocereus* was by Benson (1982), who grouped all of the red-flowered populations within the United States under a single species, *E. triglochidiatus* Engelm. in F. A. Wislizenus. Since Benson's treatment, other authors reported on the section (Taylor 1985; Ferguson 1989) but did not use biosystematic approaches. Recent taxonomic, cytological, and floral investigations have led specialists to separate Benson's North American *E. triglochidiatus* into at least five species, *E. arizonicus*, *E. coccineus* Engelm. in F. A. Wislizenus, *E. santaritensis* W. Blum & Rutow, *E. triglochidiatus*, and *E. yavapaiensis* M. A. Baker (Hoffman 1992; Blum et al. 1998; Zimmerman & Parfitt 2003; Baker 2006). The primary rationale for splitting *E. triglochidiatus* into several species is the occurrence of polyploidy correlated with morphology, geographic distribution, and floral dimorphism (Table 1). *Echinocereus arizonicus* represents smooth-spined, diploid, perfect-flowered populations from the Sonoran-Chihuahuan Desert interface; *E. triglochidiatus* represents papillate- [*E. triglochidiatus* subsp. *mojavensis* (Engelm. & Bigelow) W. Blum & Michael Lange] or angular-spined (*E. triglochidiatus* subsp. *triglochidiatus*), diploid, perfect-flowered, populations from the Mojave Desert, California east to northern New Mexico and north into Utah and Colorado; *E. coccineus* represents smooth to papillate-spined, tetraploid, florally dimorphic populations from southern Utah south into the mountains of Arizona and from southern Colorado south into Texas and southern Chihuahua; *E. santaritensis* W. Blum & Rutow represents tetraploid, perfect-flowered, populations from southern Arizona, and *E. yavapaiensis* hexaploid, florally dimorphic, populations from central Arizona. Several taxa endemic to Mexico remain poorly understood. For a synopsis of chromosome numbers in *Echinocereus*, section *Triglochidiatus*, see Cota and Philbrick (1994) and Baker (2006).

Nomenclature herein follows that of Blum et al. (1998). Three taxa are recognized within *E.*

TABLE 1. CURRENT TAXONOMIC STATUS OF *ECHINOCEREUS*, SECTION *TRIGLOCHIDIATUS* FOR POPULATIONS IN THE UNITED STATES AS RECOGNIZED BY ZIMMERMAN & PARFITT (2003) AND BAKER (2006).

Taxon	Spine surface	Ploidy level	Flowers	Status in the current multivariate analysis
E. arizonicus	smooth-spined	diploid	perfect	Analyzed
E. triglochidiatus subsp. *mojavensis*	papillate-spined	diploid	perfect	Analyzed as an outgroup
E. triglochidiatus subsp. *triglochidiatus*	angular-spined	diploid	perfect	Analyzed as an outgroup
E. santaritensis	smooth-spined	tetraploid	perfect	Analyzed as an outgroup
E. coccineus	smooth to papillate-spined	tetraploid	dimorphic	Not included, see Baker 2006
E. yavapaiensis	smooth-spined	hexaploid	dimorphic	Not included, see Baker 2006

arizonicus, *E. arizonicus* subsp. *arizonicus*, *E. arizonicus* subsp. *nigrihorridispinus* W. Blum & Rutow, and *E. arizonicus* subsp. *matudae* (Bravo-Hollis) Rutow. According to Blum et al. (1998), *E. arizonicus* subsp. *arizonicus* occurs in Cochise, Gila, Graham, Pima, and Pinal Counties, Arizona, and is characterized as having 7–13 radial spines and 1–4 central spines per areole and stems with 8–11 ribs; *E. arizonicus* subsp. *nigrihorridispinus* occurs in areas southeast of the distribution of *E. arizonicus* subsp. *arizonicus*, in southern Arizona, southwestern New Mexico, and northern Chihuahua and is characterized as having 10–14 radial spines and 3–8 central spines per areole and stems with 10–13 ribs; *E. arizonicus* subsp. *matudae* occurs northwestern Chihuahua and is characterized as having 7–11 radial spines and 1–4 central spines per areole and stems with 6–8 ribs.

METHODS

Twenty one continuous characters (Table 2) were measured for at least 30 mature individuals from six populations of *E. arizonicus*, two of *E. triglochidiatus* subsp. *triglochidiatus*, four of *E. triglochidiatus* subsp. *mojavensis*, and three of *E. santaritensis* (Fig. 1, Table 3). Because of permitting constraints, stem characters only were measured for the only known population of *E. arizonicus* subsp. *matudae* (Bravo-Hollis) Rutow. For statistical purposes, the assumption was made that all individuals measured within each population belonged within a single taxon. Although it is possible that individuals of more than one taxon occurred within the vicinity of any one study population, there were no locations where this was apparent from the physiognomy of the individuals present.

TABLE 2. LIST OF CHARACTERS USED IN THE ANALYSIS. Except for STEML, three measurements were made for each character per individual. The youngest fully mature areoles were chosen for stem measurements.

Character	Explanation
STEML	Length of longest stem from ground level
STEMDIA	Average stem diameter
NRIBS	Average number of stem ribs (costae)
DBTWARLS	Average distance between stem areoles
NCENTRALS	Average number of central spines per stem areole
NRADIALS	Average number of radial spines per stem areole
LRADIALS	Average length of radial spines per stem areole
LCENTRALS	Average length of central spines per stem areole
THKNCNTR	Greatest thickness of central spine (just above the swollen base) per stem areole
FLRL	Flower length from base of pericarp to tip of longest tepal
FLRWIDTH	Flower width from tepal tip to tepal tip
OUTSDIA	Outside diameter of throat of pericarp at constriction just above ovary
AXIALL	Axial length of pericarpal pith between ovary and base of pericarp
LTOUPPER	Length of pericarp from base to uppermost areole
NTEPALS	Number of tepals, excluding those with areoles at their base
STYLEDIA	Diameter of style at midpoint.
SPINEL	Length of longest within uppermost areole of pericarp
STYLEL	Length of style from its base to bottom of stigma
NCTRYDIA	Diameter of nectar chamber
OVARYL	Length of ovary
STAMENL	Length of stamens collectively

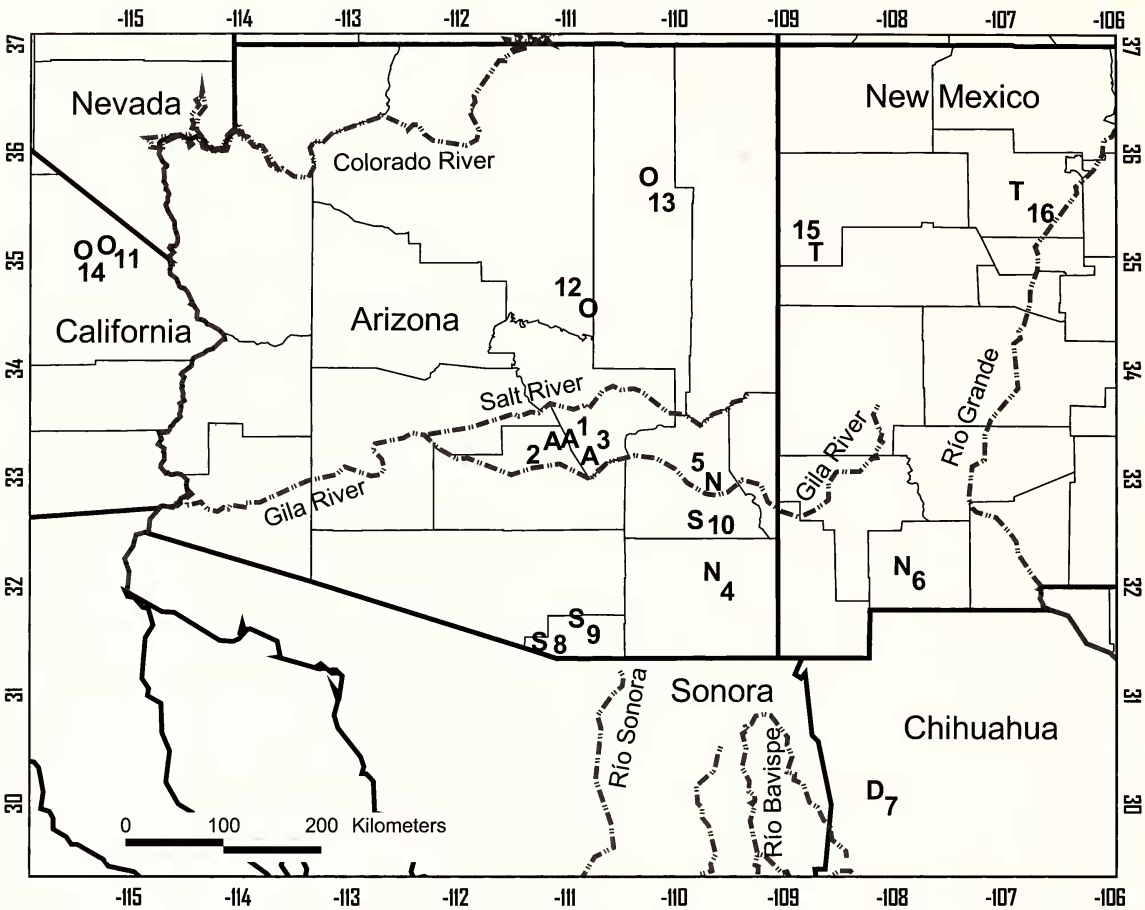

FIG. 1. Locations of study sites for populations of *Echinocereus* section *Triglochidiatus*. Numbers next to symbols refer to those of populations in Table 1.

Principle component analysis (PCA) (Systat7, SPPS Software Inc. 2000) was used to assess the taxonomic values of characters and to assign populations of Arizona and New Mexico populations of *E. arizonicus* to either *E. arizonicus* subsp. *arizonicus*, or *E. arizonicus* subsp. *nigrihorridispinus*. This was done by comparing individuals within unknown populations to those of the two type localities. In order to assess the taxonomic value of groups of variables (primarily stem characters vs. flower characters), PCA was first performed on all characters of populations of all three perfect-flowered species, and then performed using flower characters and stem characters alone. Varimax rotation was used to improve the interpretability of the scatter diagrams. The clustering algorithm unweighted pair group method with arithmetic mean (UPGMA) was performed with NTSYS® 2.1e (Rohlf 2000) to compare phenetic distance among populations of *E. arizonicus* and the outgroup, *E. triglochidiatus* subsp. *mojavensis*. This outgroup was selected because it was the only other diploid taxon for which at least three populations had been measured.

MANOVA (SPSS10) was used to test the assumptions of multivariate statistics and to test the significance of characters among taxa. Data were transformed, as necessary, to meet multivariate assumptions. Not all variables met homogeneity of variance assumptions after transformations. Also, the assumption of homogeneity of covariance matrices could not be met (Box's M test, $P < 0.001$). The Box's M test, however, is generally too strict with the large sample sizes generally necessary for multivariate applications of ANOVA (Tabachnick 2001).

Discriminant analysis (DA; SPSS10) was used to test for the correct classification of individuals within their respective taxa. Because of the small sample size, individuals of *E. arizonicus* subsp. *matudae* were not included in the analysis. Nine individuals were identified as multivariate outliers (Mahalanobis distance-squares from group means with $P < 0.001$) and were deleted from the analysis. A permit (TE-844147) for collecting flowers from individuals of *E. arizonicus* was issued by the U. S. Fish and Wildlife Service, Southwest Regional Office, Albuqerque, New Mexico.

TABLE 3. LOCATIONS OF POPULATIONS (TYPE LOCALITIES IN BOLD, CHROMOSOME DETERMINATIONS FROM BAKER [2006]).

Pop. No.	Taxon	Locale	*n*	Latitude, longitude	Elev. (m)	Collector and number
1	*E. arizonicus* subsp. *arizonicus*	**Top of the World, Gila CO., AZ**	11	33° 21.3′ 110° 58.4′	1395	*MAB 13781.1*
2	*E. arizonicus* subsp. *arizonicus*	N of Oak Flat, Pinal Co., AZ	11	33° 20.5′ 111° 02.3′	1400	*MAB 13782.1*
3	*E. arizonicus* subsp. *arizonicus*	El Capitan, Gila Co., AZ	11	33° 12′ 110° 47′	1600	*MAB 13803*
4	*E. arizonicus* subsp. *nigrihorridispinus*	Dos Cabezas, Cochise Co., AZ	11	32° 10.7′ 109° 38.9′	1500	*MAB 13748, 13749*
5	*E. arizonicus* subsp. *nigrihorridispinus*	N of Safford, Graham Co., AZ	11	32° 59′ 109° 39′	1460	*MAB 11623*
6	*E. arizonicus* subsp. *nigrihorridispinus*	**W of Deming, Luna Co., NM**	11	32° 13′ 107° 54	1460	*MAB 13958*
7	*E. arizonicus* subsp. *matudae*	**Casa Grandes, Chihuahua, Mexico**	11	30° 08.3′ 108° 09.6′	2200	*MAB 14339.1*
8	*E. santaritensis*	Ruby, Santa Cruz Co., AZ	22	31° 28.1′ 111° 13.5′	1360	*MAB 13422*
9	*E. santaritensis*	**Madera Canyon, Santa Cruz Co., AZ**	22	31° 42.7–43.7′ 110° 52.3–53.9	1480–2210	*MAB 13734, 13736, 13737, 13783*
10	E. santaritensis	Mt. Graham, Graham Co., AZ	22	32° 37′ 109° 49′	2525	*MAB* 13810
11	*E. triglochidiatus* subsp. *mojavensis*	**N of Hackberry Mtn., San Bernardino Co., CA**	11	35° 09.3′ 115° 13.4′	1335	*MAB 13706*
12	*E. triglochidiatus* subsp. *mojavensis*	Chevelon Canyon, Coconino Co., AZ	11	34° 35.6′ 110° 47.4′	1950	*MAB 13792*
13	*E. triglochidiatus* subsp. *mojavensis*	Keams Canyon, Navajo Co., AZ	11	35° 47′ 110° 14′	1895	*MAB 13626*, 13796
14	*E. triglochidiatus* subsp. *mojavensis*	**Black Canyon, San Bernardino Co., California. (type locality of E. sandersii Orcutt**	11	35° 07′ 115° 24′	1600	*MAB 13957*
15	*E. triglochidiatus* subsp. *triglochidiatus*	**Zuni, McKinley Co., NM (type locality of C. gonacanthus)**	11	35° 04.5′ 108° 42.9′	2055	*MAB 13812.2*
16	*E. triglochidiatus* subsp. *triglochidiatus*	Zia, Sandoval Co., NM	11	35° 39′ 106° 52′	1975	*MAB 13553*, 13553.1

Results

Principle Components Analysis (PCA)

Flower characters dominated the first two components of the PCA analysis that included all characters (Table 4). When components one and two were plotted together (not shown), however, there was a poor grouping of individuals within their respective taxa. Component three, which also explained a large percent of the total variance, had a stronger loading for stem characters. When components one and three were plotted together, individuals of the three taxa began to resolve but there remained a great deal of overlap (Fig. 2). For the PCA using only flower characters, none of the components adequately grouped individuals into species.

As with the interspecific analysis, stem characters discriminated individuals among taxa of *E. arizonicus* better than flower characters. A scatterplot of the first two components of PCA defined two groups that maintained the identity of individuals within populations (Fig. 3). One group was defined by populations one, two, and three, and the other group by populations four, five, and six. The first group contained the type locality for *E. arizonicus* subsp. *arizonicus* (population one) and the second for *E. arizonicus* subsp. *nigrihorridispinus* (population six). The highest loadings in the first component were for length of both central and radial spines, number of central spines, and stem diameter (Table 5). The highest loadings in the second component were for the distance between areole, thickness of central spine, and stem diameter.

Descriptive statistics, based on the defined populations, are presented in Table 6. Those for outgroups are presented in Table 7.

Unweighted Pair Group Method with Arithmetic Mean (UPGMA)

Results from a UPGMA analysis of stem characters for *Echinocereus arizonicus* with *E. triglochidiatus* subsp. *mojavensis* as an outgroup indicated that all populations were placed correctly within their respective taxa (Fig. 4). As expected, the outgroup (populations 11–14) was placed with the greatest phenetic distance with respect to populations within *E. arizonicus*. Populations of both *E. arizonicus* subsp. *arizonicus* (populations 1–3) and *E. arizonicus* subsp. *nigrihorridispinus* (populations 4–6) were distinctly grouped and the single population of *E. arizonicus* subsp. *matudae* (population 7) placed basally to either of the other two subspecies.

Multivariate Analysis of Variance (MANOVA)

Individuals of *E. arizonicus* subsp. *arizonicus*, as a group, possessed seven characters with distinct means: stem length, stem diameter,

Table 4. Component Loadings for all Characters of PCA with Varimax Rotation of Populations of *E. arizonicus* (Excluding *E. arizonicus* subsp. *matudae*), *E. santaritensis*, and *E. triglochidiatus*. For translation of character acronyms, see Table 1.

	Component				
	1	2	3	4	5
STYLEL	0.9	0.0	−0.1	0.0	0.0
FLRL	0.9	−0.2	0.0	−0.0	0.2
STAMENL	0.8	0.1	0.1	−0.1	−0.3
LTOUPPER	0.8	0.2	−0.1	−0.2	0.3
NRADIALS	0.0	0.9	0.0	−0.1	0.0
NCENTRALS	0.1	0.9	0.0	−0.1	−0.1
DBTWARLS	0.1	−0.8	0.1	0.3	−0.1
NRIBS	−0.0	0.8	0.0	0.1	0.3
OVARYL	0.4	−0.5	0.1	−0.1	0.3
NCTRYDIA	−0.1	0.0	0.9	−0.1	−0.1
OUTSDIA	0.0	0.1	0.8	0.1	0.1
STYLEDIA	0.0	−0.0	0.6	−0.0	0.0
LCENTRALS	−0.1	0.1	−0.0	0.9	−0.1
LRADIALS	−0.1	−0.4	−0.0	0.8	0.2
AXIALL	0.4	0.1	−0.2	−0.2	0.7
NTEPALS	0.0	0.0	0.3	0.3	0.6
STEMDIA	0.1	−0.1	0.2	−0.2	0.0
STEML	−0.1	0.3	0.1	0.1	0.2
THKNCNTR	−0.0	−0.1	0.2	0.2	−0.4
FLRWIDTH	0.5	−0.0	0.3	0.2	0.2
SPINEL	0.2	0.5	0.1	0.4	−0.0
	Percent of total variance explained				
	17.0	17.8	10.3	9.8	7.2

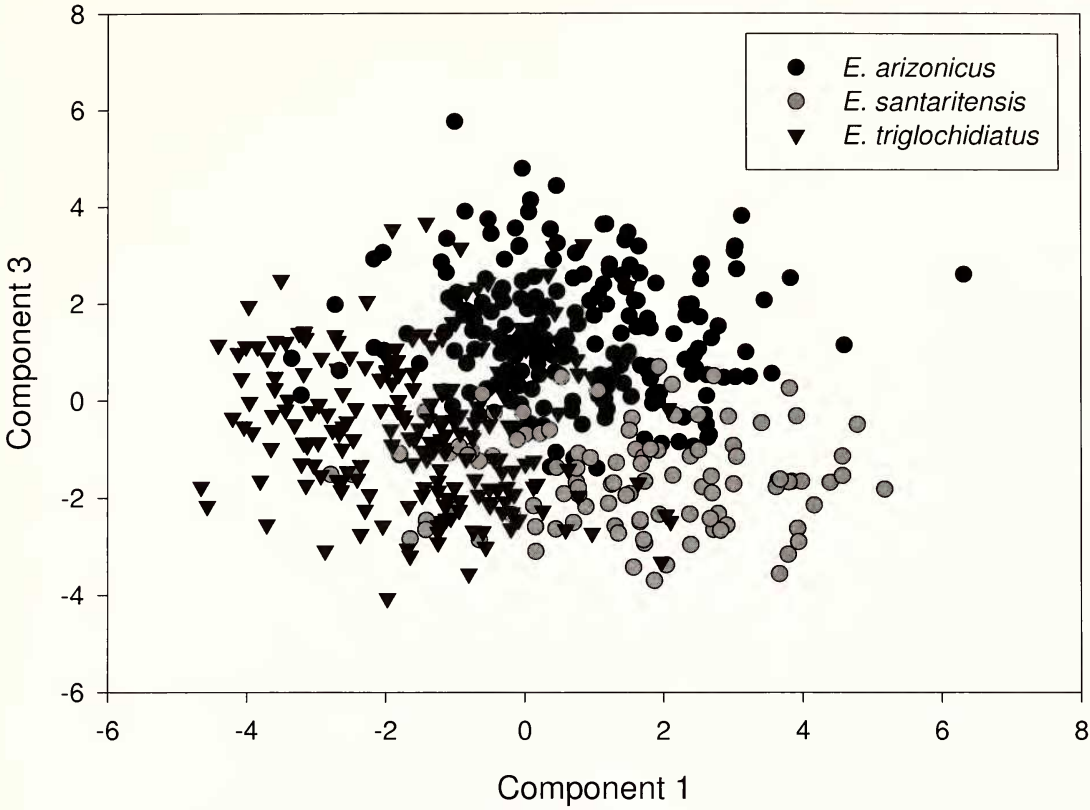

FIG. 2. Scatterplot of components 1 and 3 for PCA with varimax rotation using all characters for individuals of *E. arizonicus*, *E. santaritensis*, and *E. triglochidiatus*.

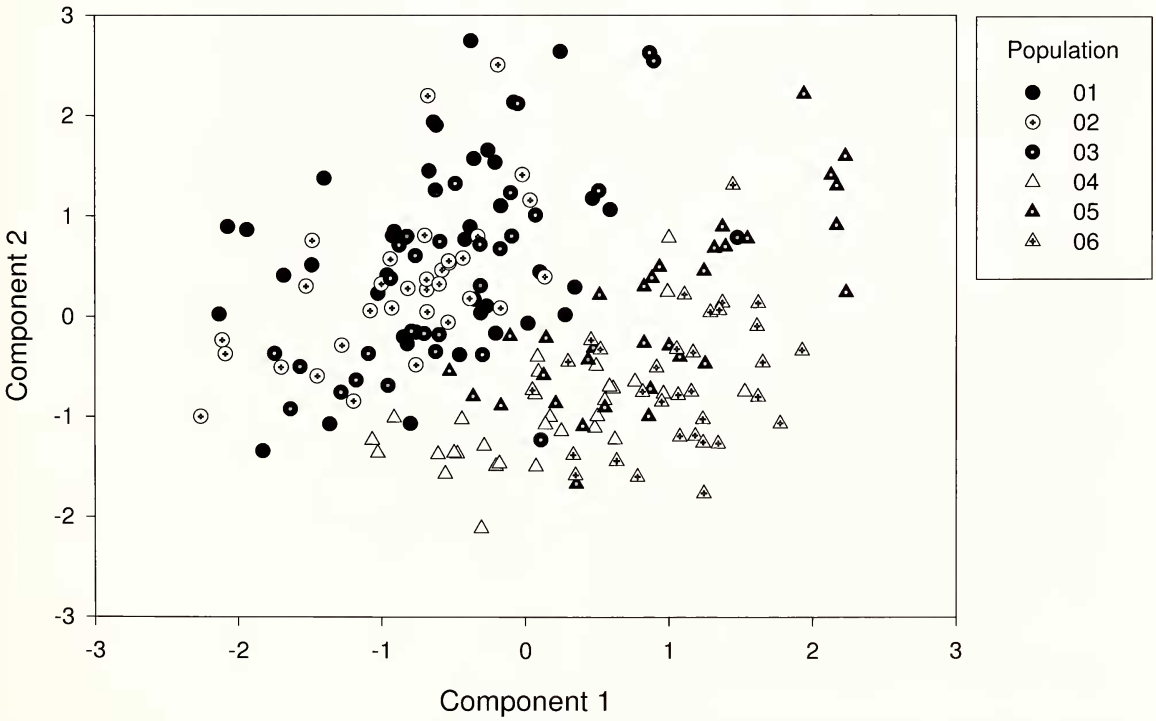

FIG. 3. Scatter plot of first two components of PCA with varimax rotation including stem characters for populations of *E. arizonicus*, excluding the one population of *E. arizonicus* ssp. *matudae*.

TABLE 5. COMPONENT LOADINGS FOR STEM CHARACTERS OF PCA WITH VARIMAX ROTATION OF POPULATIONS OF *E. ARIZONICUS*, EXCLUDING THAT OF *E. ARIZONICUS* SUBSP. *MATUDAE*.

	Component		
	1	2	3
NCENTRALS	0.8	−0.1	−0.1
LCENTRALS	0.8	−0.3	0.4
NRADIALS	0.8	0.0	0.0
LRADIALS	0.7	−0.3	0.4
DRIBS	0.6	−0.1	−0.3
STEML	−0.0	0.8	−0.2
STEMDIA	−0.4	0.8	0.2
DBTWARLS	0.0	0.7	0.5
THKNCNTR	−0.0	0.1	0.8
	Percent of total variance explained		
	30.7	20.7	16.6

distance between areoles, number of central spines, number of radial spines, length of pericarp, and style diameter (Table 8). Individuals of *E. arizonicus* subsp. *nigrihorridispinus*, as a group, possessed ten characters with distinct means: stem length, number of ribs, distance between areoles, number of centrals, number of radials, length of radials, flower length, pericarp spine length, style length, and ovary length (Table 8).

Discriminant Analysis

Discriminant analysis correctly classified 97.8% of the original grouped cases that included all of the study taxa (Table 9). Individuals of *E. arizonicus* subsp. *arizonicus* were classified correctly 97.0%, with 3.0% incorrectly classified as *E. arizonicus* subsp. *nigrihorridispinus*. Individuals of *E. arizonicus* subsp. *nigrihorridispinus* were correctly classified 94.7%, with 2.1% incorrectly classified as *E. arizonicus* subsp. *arizonicus* and 3.2% as *E. santaritensis*. A single individual (1%) of *E. santaritensis* was misclassified as *E. arizonicus* subsp. *nigrihorridispinus* and one as *E. triglochidiatus* subsp. *mojavensis*. Within *E. triglochidiatus*, only a single individual was misclassified, which was between the two subspecies. All between group correlations were highly significant (Table 10). The jackknifed classification matrix showed a one percent reduction in correct classification among each group.

Discussion

Phenetic analysis presented herein supports the recognition of at least two infraspecific taxa within *E. arizonicus*: *E. arizonicus* subsp. *arizonicus* and *E. arizonicus* subsp. *nigrihorridispinus*. Although PCA shows incomplete interspecific resolution among the species sampled, there were significant differences in means for several morphological characters between *E. arizonicus* subsp. *arizonicus* and *E. arizonicus* subsp. *nigrihorridispinus*. Morphological differences coupled with allopatric geographic distribution have long been considered basic criteria for the recognition of two separate subspecies (Stebbins 1950; Lawrence 1951). Most of the known geographical distribution for *E. arizonicus* is represented by *E. arizonicus* subsp. *nigrihorridispinus*, which was the most variable subspecific taxon within the species in terms of the diagnostic stem characters. Individuals of *E. arizonicus* subsp. *arizonicus*, which have a limited geographic range, were more variable with respect to most flower characters.

Populations of *E. arizonicus* subsp. *arizonicus* differed significantly from those of *E. arizonicus* subsp. *nigrihorridispinus* in the means of most characters measured (Table 8). However, as shown by PCA, flower characters, as a group, were not generally diagnostic within the perfect-flowered taxa as a whole and no single flower character appeared to be useful in separating populations of *E. arizonicus* subsp. *arizonicus* from those of *E. arizonicus* subsp. *nigrihorridispinus*. Although stem characters were shown to be more diagnostic than flower characters, the former tend to be more affected by factors of age and environment. Stem diameter, for example, should be avoided as a key character because of its correlation with available water. Although age is generally a critical factor in stem length, stem length is mostly determinate within section *Triglochidiatus* because of its cespitose habit. In addition, the effects of age were minimized in the present study by the measurement of only mature individuals. Diagnostic characters that are less affected by age and environment are number of ribs, number and length of central spines, and number and length of radial spines. Although even these characters may be affected by etiolation, no individuals occurring in deep shade were included in the present study.

The geographic ranges, as defined herein, of *E. arizonicus* subsp. a*rizonicus* and *E. arizonicus* subsp. *nigrihorridispinus* differs from that of Blum et al. (1998) in that populations of *E. arizonicus* subsp. a*rizonicus* are more restricted.

Data herein were not sufficient to adequately evaluate the taxonomic circumscription of *E. arizonicus* subsp. *matudae*. Although individuals within the single known population possessed the fewest ribs, greatest distance between areoles, and fewest central and radial spines in comparison to those of the other two subspecies, additional populations of *E. arizonicus* subsp. *matudae*, should be sought and measured in order to properly address morphological variation throughout its range.

TABLE 6. DESCRIPTIVE STATISTICS OF *E. ARIZONICUS*.

Character	*E. arizonicus* subsp. *arizonicus*					*E. arizonicus* subsp. *nigrihorridispinus*					*E. arizonicus* subsp. *matudae*				
	N	Min	Max	0	SD	N	Min	Max	0	SD	N	Min	Max	0	SD
STEML	104	14	48	29.6	7.9	96	13	47	25.2	6.6	35	8.5	39.0	23.1	7.8
STEMDIA	104	5.7	10.3	8.1	1.0	96	3.7	8.8	6.1	0.9	35	5.6	9.7	7.8	1.0
NRIBS	104	7	11	8.8	0.6	96	8	12.7	9.6	0.7	35	6.0	8.3	7.1	0.5
DBTWARLS	104	9	18.7	13.6	2.3	96	6.7	18	11.5	2.4	35	11.7	27.7	20.1	3.4
NCENTRALS	104	1	5	2.9	0.9	96	2	6	4.0	0.7	35	0.7	3.0	1.6	0.7
NRADIALS	104	5	12.3	9.1	1.3	96	7.3	13	10.2	1.4	35	5.3	10.3	7.6	1.0
LRADIALS	104	9	24.7	12.4	2.5	96	9	31.3	18.7	4.7	35	13.7	29.7	20.9	4.2
LCENTRALS	104	15.3	58.3	26.0	7.2	96	21.3	59	40.5	8.8	35	21.0	52.3	31.6	6.0
THKNCNTR	104	0.62	1.37	0.95	0.15	96	0.53	1.53	0.88	0.18	35	0.59	1.67	1.04	0.19
FLRL	104	47	93.3	67.7	9.0	96	46.3	74.3	62.5	5.07	2	56.0	78.0	67.0	15.6
FLRWIDTH	104	33.3	54.3	42.4	4.6	96	30	55	40.9	5.4	2	39.0	43.7	41.4	3.3
OUTSDIA	104	8.7	16	12.0	1.6	96	9	17	11.8	1.4	2	16.0	16.0	16.0	0.0
AXIALL	104	3	29	12.8	5.2	96	2.7	16	7.5	3.6	2	4.0	6.0	5.0	1.4
LTOUPPER	104	25	58.3	39.5	6.2	96	26	46	37.4	4.1	2	30.0	49.0	39.5	13.4
NTEPALS	104	17	37	22.9	3.0	96	17	33	23.5	2.8	2	22.0	25.7	23.8	2.6
STYLEDIA	104	1.20	2.37	1.74	0.24	96	1.07	2.15	1.61	0.20	2	1.90	2.05	1.98	0.11
SPINEL	104	7	15.5	10.6	1.9	96	7	19	11.7	2.2	2	7.0	9.0	8.0	1.4
STYLEL	104	31.7	53.7	43.4	5.3	96	28.3	50.7	41.0	3.8	2	37.0	49.7	43.4	9.0
NCTRYDIA	104	2	7.5	3.6	1.1	96	2	6	3.3	0.6	2	4.0	4.0	4.0	0.0
OVARYL	104	3	11.3	7.2	1.8	96	2.5	12	5.8	2.0	2	4.0	8.3	6.2	3.0
STAMENL	104	27	50.3	39.5	5.4	96	26	47.3	37.8	4.3	2	32.0	42.0	37.0	7.1

TABLE 7. DESCRIPTIVE STATISTICS OF OUTGROUPS.

Character	*E. triglochidiatus* subsp. *mojavensis*					*E. triglochidiatus* subsp. *triglochidiatus*					*E. santaritensis*				
	N	Min	Max	0	SD	N	Min	Max	0	SD	N	Min	Max	0	SD
STEML	132	5.0	45.0	21.1	10.0	73	6.0	25.0	13.2	4.2	105	8.0	36.0	18.4	6.9
STEMDIA	132	4.8	9.0	6.1	0.9	73	5.0	9.0	6.4	1.0	105	4.0	7.0	5.4	0.7
NRIBS	132	7.7	13.0	9.0	0.7	73	5.0	8.5	6.8	0.6	105	8.0	12.0	9.8	0.8
DBTWARLS	132	7.7	25.7	16.4	4.3	73	14.0	36.7	22.8	5.6	105	6.0	14.0	9.4	1.7
NCENTRALS	132	0.0	2.0	1.0	0.4	73	0.0	1.0	0.4	0.4	105	1.0	5.0	3.5	0.7
NRADIALS	132	4.3	9.0	6.8	1.2	73	1.7	6.7	4.4	1.2	105	7.0	12.0	9.5	1.1
LRADIALS	132	13.0	62.7	31.0	10.3	73	0.8	37.7	22.0	6.2	105	7.7	34.3	16.5	4.9
LCENTRALS	130	18.3	83.7	40.9	12.3	42	14.3	58.3	29.1	9.2	105	17.7	49.0	31.3	8.3
THKNCNTR	130	0.3	1.2	0.7	0.2	47	.40	1.74	0.91	0.26	105	0.33	1.05	0.60	0.16
FLRL	132	48.5	88.3	65.6	7.3	73	54.7	87.0	70.4	6.7	105	47.0	115.5	67.5	9.0
FLRWIDTH	132	32.0	60.7	40.7	6.2	73	33.0	50.7	41.8	4.4	105	32.0	56.7	42.1	5.5
OUTSDIA	132	7.0	14.7	10.9	1.7	73	8.0	13.7	10.6	1.1	105	7.3	12.7	9.8	1.1
AXIALL	132	3.0	23.0	12.0	4.6	73	3.0	20.0	6.8	3.4	105	8.0	31.5	13.6	3.2
LTOUPPER	132	22.7	55.0	37.0	5.5	72	27.5	53.0	37.2	4.7	105	31.0	71.5	44.7	6.6
NTEPALS	132	16.3	32.5	24.0	3.1	73	15.7	29.0	22.4	2.7	105	16.5	27.5	22.7	2.0
STYLEDIA	132	1.10	2.10	1.53	0.21	73	1.15	2.01	1.59	0.18	105	1.10	1.90	1.47	0.18
SPINEL	132	6.3	16.7	9.9	1.9	73	5.0	15.0	8.4	2.3	105	6.7	16.7	10.5	1.7
STYLEL	132	26.5	53.3	42.8	5.2	73	37.0	56.7	46.0	4.2	105	27.5	69.0	48.6	6.5
NCTRYDIA	132	1.7	5.7	3.1	0.8	73	2.0	5.7	3.2	0.7	105	1.8	5.5	3.1	0.7
OVARYL	132	3.5	16.3	7.6	2.0	73	4.3	13.7	8.9	2.2	105	3.7	17.5	6.6	1.9
STAMENL	132	26.5	50.7	35.5	3.8	73	32.5	52.0	40.1	4.1	105	21.0	56.5	38.2	6.9

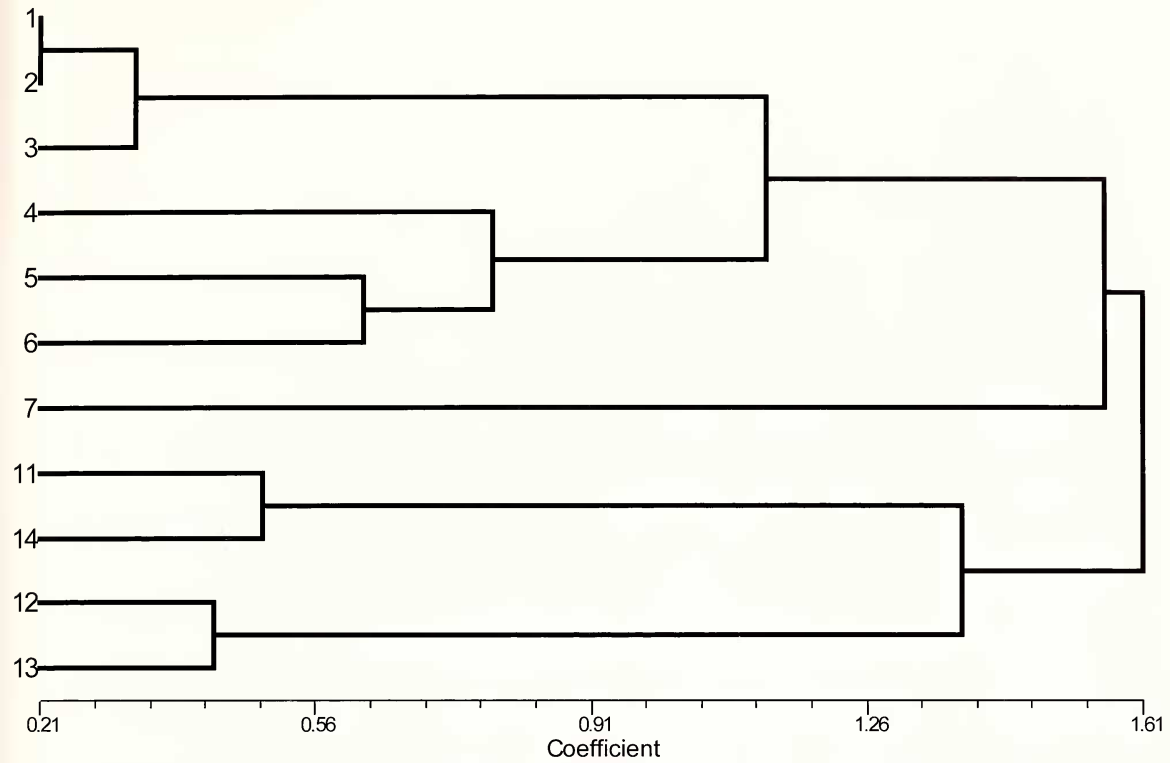

FIG. 4. Phenogram from UPGMA including populations of *E. arizonicus* and *E. triglochidiatus* ssp. *mojavensis*. Matrix composed of mean values for each character.

Similarly, data were not adequate for the assessment of the taxonomic circumscription of the two subspecies of *E. triglochidiatus*, primarily because of the lack of data from the type locality for *E. triglochidiatus* ssp. *triglochidiatus*. Furthermore, UPGMA suggests that *E. triglochidiatus* subsp. *mojavensis* may be composed of more than one taxonomically definable group, a western

TABLE 8. SELECTED HOMOGENEOUS SUBSETS FROM MANOVA SIGNIFICANCE (DUNCANS MULTIPLE RANGE TEST) WHERE $P > 0.02$.; SUBSET A HAS THE SMALLEST MEAN VALUE AND E HAS THE LARGEST. For all subsets containing a single taxon, $p = 1.000$. 1 = *E. arizonicus* subsp. *arizonicus*, 2 = *E. arizonicus* subsp. *nigrihorridispinus*, 3 = *E. santaritensis*, 4 = *E. triglochidiatus* subsp. *mojavensis*, 5 = *E. triglochidiatus* subsp. *triglochidiatus*. See Tables 5 and 6 for specific means.

	Subset				
	A	B	C	D	E
STEML	5	3	4	2	1
STEMDIA	3	4, 2	2, 5	1	
NRIBS	5	1, 4	2	3	
DBTWARLS	3	2	1	4	5
NCENTRALS	5	4	1	3	2
NRADIALS	5	4	1	3	2
LRADIALS	1	3	2	5	4
LCENTRALS	1	5, 3	4, 2		
THKNCNTR	3	4	2, 5	5, 1	
FLRL	2	4, 3, 1	5		
OUTSDIA	3	5, 4	2, 1		
LTOUPPER	4, 5, 2	1	3		
STYLEDIA	3, 4	5, 2	1		
SPINEL	5	4	3, 1	2	
STYLEL	2	4, 1	5	3	
OVARYL	2	3	1, 4	5	
STAMENL	4	2, 3	1, 5		

TABLE 9. PREDICTED GROUP MEMBERSHIP FOR DA AMONG INDIVIDUALS WITHIN POPULATIONS PRECLASSIFIED AS *E. ARIZONICUS* SUBSP. *ARIZONICUS*, *E. ARIZONICUS* SUBSP. *NIGRIHORRIDISPINUS*, *E. SANTARITENSIS*, *E. TRIGLOCHIDIATUS* SUBSP. *MOJAVENSIS*, AND *E. TRIGLOCHIDIATUS* SUBSP. *MOJAVENSIS*. 97.8% of original grouped cases were correctly classified.

Taxon	*E. arizonicus* subsp. *arizonicus*	*E. arizonicus* subsp. *nigrihorridispinus*	*E. santaritensis*	*E. triglochidiatus* subsp. *mojavensis*	*E. triglochidiatus* subsp. *triglochidiatus*	Total
			By number of individuals			
E. arizonicus subsp. *arizonicus*	98	3	0	0	0	101
E. arizonicus subsp. *nigrihorridispinus*	2	90	3	0	0	95
E. santaritensis	0	1	102	1	0	104
E. triglochidiatus subsp. *mojavensis*				128	1	129
E. triglochidiatus subsp. *triglochidiatus*	0	0	0	0	72	72
			By percent of individuals			
E. arizonicus subsp. *arizonicus*	**97.0**	3.0	.0	.0	.0	100
E. arizonicus subsp. *nigrihorridispinus*	2.1	**94.7**	3.2	.0	.0	100
E. santaritensis	.0	1.0	**98.1**	1.0	.0	100
E. triglochidiatus subsp. *mojavensis*	.0	.0	.0	**99.2**	.8	100
E. triglochidiatus subsp. *triglochidiatus*	.0	.0	.0	.0	**100.0**	100

group represented by the type and an eastern group, perhaps represented by the basionym *Cereus mojavensis* Engelm. & J. M. Bigelow var. *zuniensis* J. M. Bigelow & Engelm, for which the type locality is in Canyon Diablo, east of Flagstaff, Arizona.

Evidence from comparative morphology and geographic distribution suggests that tetraploid populations within section *Triglochidiatus*, specifically *E. santaritensis*, probably arose from *E. arizonicus* subsp. *nigrihorridispinus*. The two taxa are morphologically similar, sympatric over much of their ranges, and are both perfect-flowered.

KEY TO THE SUBSPECIES OF *ECHINOCEREUS ARIZONICUS*

Note that populations display a high degree of morphological variability among individuals and, consequently, data from several individuals should be averaged for identification. *Echinocereus arizonicus* subsp. *matudae* is included in a somewhat preliminary sense in that additional data may be needed to address morphological variation throughout its range.

A- Stems of mature individuals with mostly 10 ribs, central spines averaging 4 in number and mostly 4 cm long or longer, radial spines

TABLE 10. BETWEEN GROUPS F-MATRIX (DF = 21, 701). $P < 0.01$ FOR ALL VALUES. Wilks' Lambda = 0.004, Approx. F = 70.2 prob < 0.00001.

Taxon	*E. arizonicus* subsp. *arizonicus*	*E. arizonicus* subsp. *nigrihorridispinus*	*E. santaritensis*	*E. triglochidiatus* subsp. *mojavensis*	*E. triglochidiatus* subsp. *triglochidiatus*
E. arizonicus subsp. *arizonicus*	0.0				
E. arizonicus subsp. *nigrihorridispinus*	36.3	0.0			
E. santaritensis	81.7	36.1	0.0		
E. triglochidiatus subsp. *mojavensis*	118.3	97.1	75.6	0.0	
E. triglochidiatus subsp. *triglochidiatus*	115.0	144.0	153.7	79.6	0.0

averaging 10 in number. Arizona: Cochise, Graham, Greenlee, Pima, and Santa Cruz Counties; New Mexico: Hidalgo and Luna counties; Mexico: probable occurrence in Sonora and Chihuahua . . . . . *E. arizonicus* subsp. *nigrihorridispinus*

AA- Stems of mature individuals with mostly 9 or fewer ribs, central spines averaging 3 or fewer in number and mostly shorter than ca. 3 cm, radial spines averaging 9 or fewer in number . . B

B- Stems of mature individuals with mostly 9 ribs, central spines averaging 3 in number, radial spines averaging 9 in number and mostly shorter than 1.3 cm. Arizona: NE Pinal and SW Gila Counties . . . . . *E. arizonicus* subsp. *arizonicus*

BB- Stems of mature individuals with mostly 7 ribs, central spines averaging fewer than 2 in number, radial spines averaging fewer than 8 in number and mostly longer than 2 cm. Mexico: Chihuahua . . . . . *E. arizonicus* subsp. *matudae*

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